

MYRMECOPHILY IN LYCAENID BUTTERFLIES  
(LEPIDOPTERA : LYCAENIDAE)

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The family Lycaenidae comprises more than a third of the total number of species of butterflies in Africa, and several new species are still being discovered every year. They are small to medium-sized butterflies and are noted for their brilliant metallic blue, red or orange coloration. However they are most famous for the association of their larvae with ants.

A remarkable number of animal species exploit the colonies of social insects in one way or another. Most do so only occasionally, functioning as casual predators or temporary nest commensals. But a great many others are dependent on social insects during part or all of their life cycles. The larvae of many lycaenids have a variety of associations with ants and are referred to as myrmecophiles. The larvae of the Lycaenidae are usually onisciform, (widest and highest in the middle, with dorsal surface gently convex, like a woodlouse), with head largely hidden beneath the prothorax. The cuticle is relatively much thicker than in other lepidopterous larvae.

Most lycaenid larvae have a median dorsal organ (honey-gland) on the seventh abdominal segment and a pair of dorsolateral eversible organs (tubercles) on either side of the eighth segment. Either or both these organs may be lacking. In addition most lycaenid larvae have small epidermal glands concentrated in certain areas that appear to produce a volatile chemical substance that attracts ants.

The honey-gland consists of a shallow, usually transverse, slit or depression near the posterior margin of the segment into which several glands discharge. The depression fills with secretion and can be partly everted by blood pressure resulting in the appearance of a droplet of fluid which is immediately consumed if ants are in attendance. Setae bordering the depression help to retain the droplet if ants are not there to take it immediately. Larvae of some species such as *Poecilmitis lycegenes* (Trimen), are dependent upon ants to remove the liquid and, in the absence of ants, the larvae become mouldy and die if the fluid is not removed artificially. On the other hand, some species that possess a honey-gland are not known to be attended by ants.

Maschwitz *et al.* (1975) analysed secretions of the honey-gland of *Lysandra hispana* H.-S. to determine the possible food content. They found that in addition to water, the main constituents of the secretion were fructose, sucrose, trehalose and glucose — the total concentration of these sugars being more than 10% (13.1% and 18.7%). The haemolymph of the caterpillars, however, had a total

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carbohydrate content of only about 2% indicating that the honey-gland concentrates the sugars in the secretions to make it more attractive as a food for the ants. Other than minor quantities of protein, only one amino acid could be detected in the secretion. They found that large larvae of *L. hispana* were able to release the secretion in intervals of less than two minutes for at least one hour. The larvae of *L. hispana* were visited regularly in the field by ants which lay trails to the caterpillars and recruit new members from their colony.

The paired tubercles of the eighth abdominal segment are each frequently set in the tip of a cylinder into which they are retracted. In this condition their position is indicated externally by a small, round, often whitish, depression, generally bordered by setae. When everted by blood pressure they are seen to carry on their surface a rosette of slender, sometimes brightly coloured spiculate setae, each associated with a gland cell. The tubercles may be individually or simultaneously everted and retracted with great speed and the setae whirled or vibrated. The tubercles generally first appear in the second instar, although in some species they may appear either earlier or later.

The function of the tubercles is still in doubt. Several authors suggested that they have an odoriferous function which might signal the presence of a honeydew-producing caterpillar to ants. It has been observed though that if ants are too persistent in their efforts to obtain secretions from the honey-gland they will be deterred by the action of the tubercles when these come into play. Clark and Dickson (1956) suggested that the tubercles could perhaps be used in the same way to prevent small insects other than ants from interfering with the honey-gland. Claassens and Dickson (1977) have made the most recent observations of importance, with respect to the tubercles of *Aloeides thyra* (L.). Although the larvae of this species are phytophagous they do, at least in the fourth to the sixth instars, remain in ants' nests under stones during the day, but come out at night to feed on their foodplants. They possess the highly evolved type of tubercle with long setae, but do not possess any honey-gland of the usual form. When studying these larvae in artificial ants' nests Claassens and Dickson noticed an excited reaction by the ants whenever the tubercles of a larva were extended, temporarily increasing the activity around the larva. The attraction is mutual since these larvae will follow the trail of the ants leading from a nest to the foodplants when they emerge from the nests at night to feed. The larvae ensure the company of the ants as they travel by rapidly and repeatedly extending and retracting their tubercles. They suggest that the tubercles produce a volatile chemical of brief effectiveness which causes the ants to act in this manner.

Henning (1980, 1983a, b) observed similar behaviour with the

closely related *Aloeides dentatis* (Swierstra). He found that the glands on the tubercles of *A. dentatis* produced a volatile chemical substance that appeared to mimic the alerting and attracting components of its host ants' alarm pheromone but not the biting markers. When the *A. dentatis* larvae extruded their tubercles and released the volatile chemical the ants within a range of 2-4cm became alerted. The ants' rate of locomotion increased; they made short fast runs with frequent changes of direction with mandibles held open and increased antennal movement. The ants within a 2cm range were also alerted but were attracted directly towards the lycaenid larvae. The ants then accompanied the *A. dentatis* larvae out of the nest to the foodplants. The alerting component of the pheromone diffuses more rapidly than the attracting component, thus accounting for the fact that the ants far from the *A. dentatis* were only alerted while the ants close to the larvae were both alerted and attracted towards them.

Hinton (1951) was the first to suggest that the epidermal glands secreted an ant attractant substance. Malicky (1969, 1970) also noticed that ants tend to palpate with their antennae certain areas of the lycaenid larvae more intensively than others. He found that these areas contain small epidermal glands that are rare or absent elsewhere. He called these glands perforated cupolas. He believed that they produce a volatile substance which releases the ants' palpation although he did not know the nature of the chemical.

Henning (1980, 1983b) carried out experiments to determine whether the association between ants and lycaenid larvae is mediated by chemical signals. He observed the ants' reactions to extracts of the lycaenid's glands impregnated onto inert material. The volatile secretions of the lycaenid's glands and those of the ants were also compared using gas chromatography. It was found that in the two myrmecophilous species studied, *A. dentatis* and *Lepidochrysops ignota* (Trimen), the epidermal glands (perforated cupolas) produced a chemical secretion which is very similar to, and appeared to mimic, the brood pheromone of their host ants. In *A. dentatis* it was also found that a second secretion produced by glands on the tubercles appeared to mimic components of the alarm pheromones of the host ant (see above).

So it appears that most lycaenid larvae have small epidermal glands concentrated in certain areas that possibly produce a volatile chemical substance that attracts ants. Some larvae also have a large dorsal honey-gland on the seventh segment which produces a substance that has been compared to the honey-dew excreted by aphids. This substance is imbibed by the ants. On the eighth abdominal segment there is often a pair of dorsolateral eversible organs (tubercles) whose possible function has caused some controversy. These may be used in some species to keep the honey-gland from being

over exploited, while in other species there can be a communicatory function.

The cuticle of lycaenid larvae is many times thicker than that of other lepidopterous larvae, which confers valuable protection against attack by ants. Furthermore, most lycaenid larvae, unlike the majority of other lepidopterous larvae, do not perform jerky lateral movements when physically disturbed. Since fast motions of this sort are very effective in releasing aggressive behaviour in ants, their absence in lycaenid larvae may be a further adaptation to their association with ants. Wilson (1971) observed that ants have excellent form vision and are especially keen at detecting moving objects. He found that workers do not respond to prey insects standing still, but ran toward them as soon as they began to move.

Larsen & Pittaway (1982) found that larvae of *Apharitis acamas* (Klug) appear to pick up the nest odour of their own particular colony of host ants which makes them unacceptable to other colonies of host ants. When they released a larva from one colony of host ants into another colony of host ants it was immediately attacked and killed by the workers.

Schroth & Maschwitz (1984) did studies on *Maculinea teleius* Bergsträsser to find out how the fourth instar larvae find their way into the nest of their host ant *Myrmica laevinodis* Nylander. They did trail-following experiments with artificially laid trails of *M. laevinodis* and demonstrated that the fourth instar larvae of *M. teleius* actively find the host nest, using the pheromone trails of the workers. They produced these artificial trails by making watery suspensions of crushed gasters of *Myrmica* workers.

Once the lycaenid larvae have been carried, or have made their way into the host nest, they become fully integrated into the colony. The lycaenid larvae are groomed and generally treated as the ants do their own brood.

Claassens (1976) observed an extraordinary behaviour pattern in which *Lepidochrysops* larvae appeared to 'lick' the host ants' legs, head and abdomen. The ants responded to this tactile stimulus by remaining motionless, or in some cases lying on their sides. Claassens examined these ants but could find nothing unusual about them which could have induced this behaviour in the larvae. This is probably a type of grooming behaviour which has also been observed in other myrmecophiles, for example, Staphylinidae and Historidae (Coleoptera). Claassens also noted that when brood was scarce in the nest *Lepidochrysops* larvae would attempt to solicit regurgitated food (trophallaxis) from the ants. The larva would lift its head from the floor of the nest so that its mouth was exposed and would approach an ant attempting to touch its mandibles with its own. Claassens says that the larvae of the host ants, *Camponotus maculatus* F., showed similar behaviour which sometimes

seemed to result in trophallaxis. Feeding of lycaenid larvae by ants has been observed in several non-South African species, including *Maculineaalcon* F. from Europe.

Ants also show considerable 'interest' in lycaenid pupae. This may also be due to the production of pheromones as the small epidermal glandular organs which produce the chemical in the larvae are also present in the pupae. The pupae of the *Lepidochrysops* have extraordinarily shaped setae, the ends of which usually appear to be covered with a shiny dried substance. The setae are hollow and the ants obtain a fluid from them which they appear to find extremely attractive. The ants also continue to visit empty pupal cases after the emergence of the imagos. Before emergence the host ants show an increased interest in the pupae. Claassens (1976) observed that they turn suddenly towards such pupae as if they had received some cue. Once an imago succeeded in breaking the pupal case during emergence, the ants were seen to seize a free edge and pull on it, apparently attempting to tear it apart so as to free the adult. This behaviour by the ants is very similar to that shown by them to emerging ant cocoons. Claassens suggest that the attractive pupal remains act as a 'decoy' allowing the emerging adult lycaenids to escape from the ants nest without being attacked or eaten, but this has not been adequately demonstrated.

The body and appendages of the newly emerged adult lycaenid are covered by a temporary coating of easily detachable scales. These scales function to prevent the ants from developing an effective attack on the delicate adult as it makes its way out of the nest. The scales are detached and adhere to any part of the ant that comes into contact with them. Scales stick to the antennae, mouth-parts and legs of the ants, which then retreat and become so fully occupied cleaning themselves that the newly emerged adult is able to escape. When the adult has made its way out of the nest, it expands its wings, and a stroke or two suffices to detach any of the temporary scales that may still remain.

Three good examples of lycaenid species which virtually cover the whole range of myrmecophilous behaviour are *Aloeides dentatis* (Swierstra), *Lepidochrysops ignota* (Trimen) and *Poecilmitis lycegenes* (Trimen).

*Aloeides dentatis* is a small butterfly, orange in colour on the upperside and red marked with black and silver on the under. The flight is short and rapid, always near the ground except when the insect is chasing others about. When disturbed it rises up from its resting spot on the ground, swiftly zigzags a few metres, and alights on the ground again. It often sits so close as almost to be trodden on by passers by.

The female oviposits two eggs in quick succession on the under surface of a leaf of the foodplant *Hermania depressa* N.E.Br. (Sterculiaceae) after she has detected the presence of the correct ant *Acantholepis capensis* Mayr. The females settle on the ground in an area and investigate the *H. depressa* plants with their antennae. They can walk for a considerable distance passing their antennae over the ground and the plants. One female was watched for 45 minutes during which time she did not take to the wing once. She walked about 3 metres and investigated numerous plants, but did not lay a single egg. After 45 minutes she came to a *H. depressa* plant near an *A. capensis* nest which was frequented by the ants. The *A. dentatis* female investigated the plant and surrounding area by slowly passing her antennae over the surface. She then climbed onto the leaves of the plant, all the time passing her antennae over the surface. She then curved her abdomen over the edge of the leaf and laid two eggs in quick succession next to each other on the under surface and then flew off. All the females observed displayed a similar behaviour pattern to the one described above. There was no actual interaction between the female and the ants and in some instances there were no worker ants present on the plant at the time of ovipositing. In these instances ants were observed on the plants before the *A. dentatis* investigated it and oviposited. It appears that something deposited by the ants may cause them to lay. This substance may well be the ants' trail pheromone.

To test the hypothesis that ants were necessary for egg laying to occur, 20 females were captured. Ten females were placed in a container with the foodplant alone, and ten with the foodplant plus ants. The result was that all ten of the females housed with *H. depressa* and the ants laid at least two eggs, while none of those placed with the foodplant alone laid even a single egg. Three of the females outlived the ants placed with them, but continued to lay even though the ants were no longer present.

The eggs take from 13-22 days to hatch. All the larval instars are rather similar in appearance. The retractile tubercles are white and are clearly visible, even to the naked eye. The honey-gland on the seventh segment is absent in this species.

The first and second instars eat only the surface of the leaf, leaving patches or short furrows. The third instar starts to feed on the margins of the leaves. During this period the larvae are attended by the ant *A. capensis*. The first two instars do not appear to leave the foodplant as they are small enough to be concealed amongst the leaves. The third instar larvae are usually absent from the foodplants during the day as they shelter with the ant brood inside the nest.

The third to sixth larval instars shelter during the day in the nest of the ant *A. capensis*. The larvae tend to congregate together in

the nest often with the brood of the ants. The largest number of larvae found in a single nest was four. The *A. dentatis* larvae usually remained motionless in the nest while the ants constantly attended them, either stroking them slowly with their antennae or just standing on or near them. The droppings of the larvae were removed by the ants to the 'refuse pile'.

The *A. dentatis* larvae usually left the nest between 1900 and 2100 hours to feed. Often the larvae would leave the nest together, following one behind the other. They appear to follow the odour trails laid by the ants in their foraging. Once the *A. dentatis* larvae started moving they repeatedly extruded their tubercles, usually both at the same time. This alerted the attendant ants. They would make short fast runs with frequent changes of direction around and over the larvae, with mandibles held open and with increased antennal movement. The focus of attention was the tubercles. Several workers usually ran up to the tubercles and if the long crowning setae were touched by the ants' antennae, they were retracted immediately.

As the *A. dentatis* larvae made their way along the odour trails towards the foodplant the tubercles were extruded at intervals keeping the ants in attendance at a high level of alertness.

During the actual feeding, when the larvae were stationary, the tubercles were not repeatedly extended and the ants in contact with them were not as alert as when they were moving. The number of ants remained relatively constant around the larvae as they fed. The activity of the ants on or close to the larvae was greater when the larvae were feeding than when they were at rest in the nest because of the occasional extrusion of the tubercles. There were usually from 3-10 ants present around each larva.

After feeding, the larvae returned to the nest by following the same pheromone trail back. This may be  $\frac{1}{2}$  to 2 hours after first leaving the nest. The ants were again kept at a high level of alertness by the extrusion of the tubercles.

The larvae appear to remain in the ants' nest over the winter months when their foodplant is not available. Fifth and sixth instar larvae found in an *A. capensis* nest in July were in a dormant state and remained so for a considerable time. The sixth (final instar) larva finally pupated in October without further feeding. The fifth instar commenced feeding at this time and finally moulted into the final instar in February of the following year. The actual duration of this instar could not be recorded, but 196 days had elapsed between the date of its discovery to the time it finally moulted. The duration of the sixth instar during the summer months is some 42 days, but is obviously much longer during the winter months when diapause takes place.

The pupae are found in the ants' nest attached by their cremal hooks on the floor of the tunnels. The pupae found so far have always been in side tunnels, away from the main brood chamber. This stage lasts some twenty days.

(to be concluded)

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## Notes and Observations

UNUSUAL EGGLAYING IN THE PEACOCK BUTTERFLY — In an interesting article, (*Ent Rec.* 98: 9-10), A. S. Pullin draws attention to the occasional habit of female small tortoiseshell butterflies of depositing their eggs on top of previously laid batches. In May 1986, I caged three female peacocks in a large bucket cage containing fresh, bushy young nettles. After one week, a typical large egg batch was laid. Within 24 hours, a fresh batch had been deposited on the basal aspect of the first batch. The second batch was normal in all respects, save its proximity to the first batch. I have never observed this behaviour before, either in the peacock or small tortoiseshell butterflies. W. E. RIMINGTON, 8 Riverside Drive, Sprotborough, Doncaster.

SOME LATE SIGHTINGS OF BUTTERFLIES AND OTHER INSECTS IN AND AROUND HAMPSHIRE DURING THE MILD AUTUMN OF 1986. — Although there were some cold nights during the first half of September, the autumn was generally most mild and it was not until the end of the first week of December that the first effective frost occurred in Hampshire; moreover, day temperatures remained unusually high and something approximating to a drought prevailed until the autumn rains arrived, in earnest, on 20th October. As a consequence, many insects lingered deep into the autumn and a greatly extended season resulted.

In terms of butterflies it appears that we had the most drawn out season since the remarkable 1975, when *Lasiommata megera*, *Pararge aegeria* and *Pieris rapae* lasted into November. In central southern England it is unusual for *Pyronia tithonus* to be seen after the first few days of September. For many years my own latest sighting was of a lone female on 11th September (1971); this 'record' was superseded on 13th September 1985 and I then considered my 1986 sighting of a very worn female on 18th September to constitute a personal nonpariel, and took pride in the fact that the butterfly was seen in my garden. Pride comes before a fall, for one was seen no later than 3rd October at Hambledon Hill, Dorset!

*Hipparchia semele* was seen on the Chalk near Wallingford, Berks, on 4th October and on the 8th on a dry heath near Farnborough, Hants. Although I have, in years long gone, seen this